

Male-biased latitudinal cline of Jungle Crows on Sakhalin Island

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Abstract. Sakhalin Island, one of the largest islands in the Russian Federation, is isolated from the Eurasia continent by the Tatarsky Strait and from Japan's Hokkaido Island by La Pérouse Strait. The island stretches in a meridional direction roughly 950 km and has maximum and minimum widths of 160 km and 26 km respectively. The Jungle Crow (*Corvus macrorhynchos*) inhabits the entirety of Sakhalin Island. No geographic barrier exists that would prevent crows from migrating between the southern and northern portions of the island. The entire island is in the oceanic climate zone and has a temperature seasonality that shows a clear gradation in the meridional direction, becoming progressively larger from south to north. The island thus has potential utility for addressing latitudinal variation in the Jungle Crow's morphology. The author collected the crows serially from the south end of Sakhalin Island to the north end during June-July of 2007 breeding season. Two methods – the phenetic and metric approaches – were applied in the current skull-morphology study. Three phenetic traits, metric ten traits and body mass demonstrated neither clines nor gaps in latitudinal distribution for both sexes, with the exception of all five metric traits from the bill block in the male sample set. The male-biased cline, decreasing reversely from south to north, coincided with temperature seasonality; the cline in male bill size was found to be in accordance with Allen's rule.

Key words: Allen's rule, Jungle Crow *Corvus macrorhynchos*, latitudinal cline, skull morphology, Sakhalin Island.

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I. INTRODUCTION

The Jungle Crow *Corvus macrorhynchos* WAGLER, 1827 is distributed widely across the Indomalaya and East Palearctic ecozones (Fig. 1), from Afghanistan to the Russian Far East (GOODWIN 1986; DICKINSON 2014). East Asia, its northernmost distribution range, is commonly inhabited by two sub-species: Mandshuricus Crow *C. m. mandshuricus* BUTURLIN, 1913 and Jungle Crow *Corvus m. japonensis* BONAPART, 1850 (VAURIE 1959; NECHAEV 1991). In 2015, the author and KRYUKOV studied cranio-morphological variations of Jungle Crows among four populations in East Asia: on Hokkaido Island, Sakhalin Island, the continental seaboard adjacent to the Tatarsky Strait and the west of the Sikhote-Alin Mountains. Using phenetic analysis, the authors found a geographical pat-

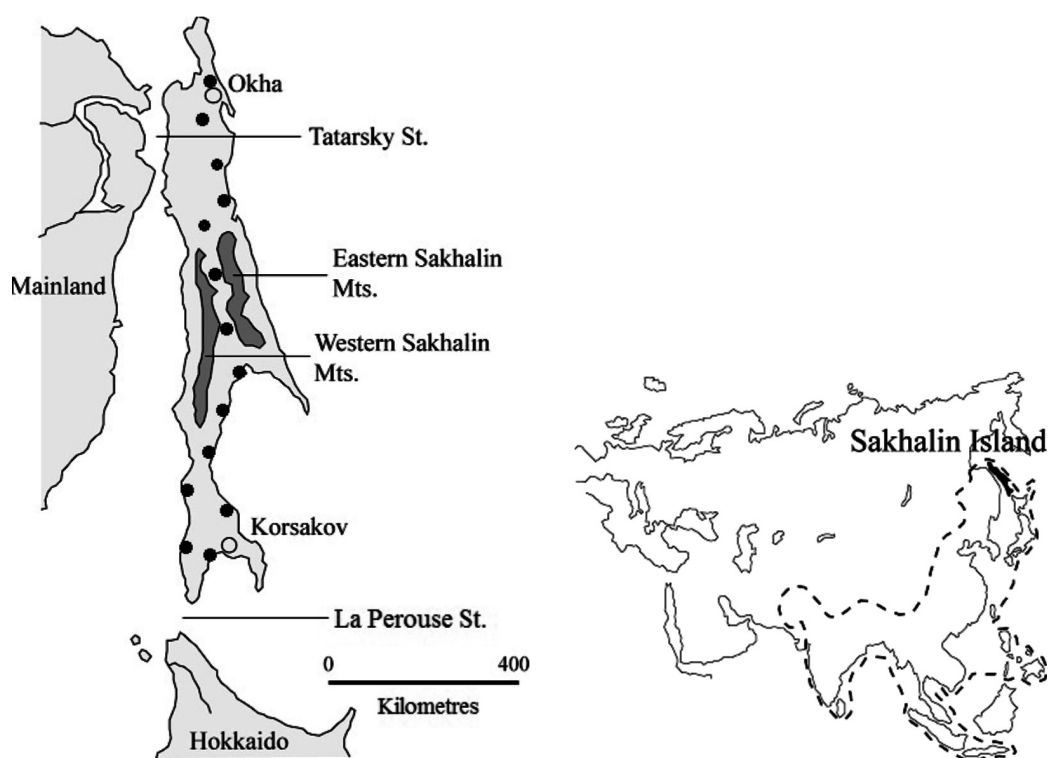


Fig. 1. Map of Sakhalin Island and its neighbours, supplemented with a map of Eurasia; the area surrounded by a dashed line is the distribution range of Jungle Crows (GOODWIN 1986). The main collection localities of Jungle Crows are indicated by solid circles.

tern of incident frequencies from two nonmetric traits that showed a significant gap between the Sakhalin and Hokkaido populations (NAKAMURA & KRYUKOV 2015); among the three Russian populations, however, no gap was found. We thus posited that a plausible border between the two sub-species could be drawn along La Pérouse Strait; cranio-metric analysis indeed decisively supported this border (NAKAMURA & KRYUKOV 2016). They revealed that two clusters may be discriminated in a principal component analysis (PCA) scatterplot diagram: a *mandshuricus* crow cluster and a *japonensis* crow cluster; the former cluster (which is composed of three sub-clusters of the Russian population) lies horizontally along PC1 axis. A longitudinal cline may be observed among these populations: body mass and skull size tend to decrease from Sakhalin Island to the interior of the continent.

Previous studies have suggested some dimorphism of Jungle Crows in Sakhalin Island: a smaller *mandshuricus* type and a larger *japonensis* type (NECHAEV 1991; IWASA et al. 2002). NAKAMURA and KRYUKOV (2016) found a few outlier plots of Sakhalin specimens in the same PCA graph that appeared far from the Sakhalin sub-cluster. These outlier plots were found in inner- and outer-continental sub-clusters. The size of the Sakhalin outliers were smaller than was the case for the majority of Sakhalin crows. The authors supposed that the smaller crows had been born in the interior and fringes of the continent but had mi-

grated to Sakhalin Island, where they were captured; they thus considered that only the *mandshuricus* crow inhabits the entirety of Sakhalin Island. KRYUKOV et al. (2012) analyzed mitochondrial-DNA *cyt-b* gene sequences from Jungle Crows, including tissue samples from Sakhalin Island; the authors were able to analyze a sufficient number of samples and determine the full sequences of *cyt-b*. They could neither discriminate haplotypes that would correspond to the *mandshuricus* or *japonensis* crow types nor find evidence that those diversifications had reached the level of speciation.

Sakhalin is one of the largest islands in the Russian Federation (Fig. 1). It is 948 km long in latitudinal direction with the minimum and maximum widths of 26 km and 160 km respectively. The island is isolated from Eurasia by the Tatarsky Strait and from Japan's Hokkaido Island by La Pérouse Strait. A plain in central Sakhalin lies between the Eastern and Western Sakhalin Mountains in the meridional direction. The island lacks a geographic barrier that would prevent crows from migrating between the southern and northern portions of the island. The entire island is in the oceanic climate zone and has a temperature that would be expected to demonstrate some gradations in the meridional direction. The island is convenient for studying latitudinal morphology variations for these reasons.

In the current morphological analysis, the author compared skull samples collected from the whole of Sakhalin Island and conducted both phenetic and metric approaches. A supplementary analysis of bioclimatic characteristics was applied to estimate the importance of environmental gradients. The author predicted that (1) phenetic traits would show no clines or gaps in latitudinal distribution; (2) body mass and cranium traits would show neither clines nor gaps in latitudinal distribution; (3) for bill traits, a latitudinal cline would occur for adapting to local environments.

II. MATERIALS AND METHODS

Jungle Crows were collected serially from the south end of Sakhalin Island to the north end during June-July of 2007 breeding season. The major sampling sites (solid marks) and geographical landmarks are shown in Fig. 1. The main sampling route was from the town of Korsakov to Okha along the meridional trunk road on both the outward and return trips. The author and his assistant drove nearly 2,000 km and collected 76 Jungle Crows (localities and specimens' number are given in the Appendix). The majority of morphological studies in the ornithology field measure skins, but because the feathers of skin specimens would prevent accurate head measurements (head length, total culmen length, etc.), the author determined that skull specimens would offer more measurable traits than skin specimens. He applied the tongue coloration method to assess age before cleaning (SVENSSON 1992). Twelve juvenile skulls were excluded. One heavily damaged male skull was not used in the cranio-metric analysis.

The author conducted the phenetic approach in parallel with the ordinary metric approach. In physical anthropology, this nonmetric approach has proven effective for establishing relationships among human populations. Comparing the incidence patterns of the supraorbital foramen and the hypoglossal canal bridge between 71 populations, DODO and SAWADA (2010) succeeded in depicting the relationships among all major human popula-

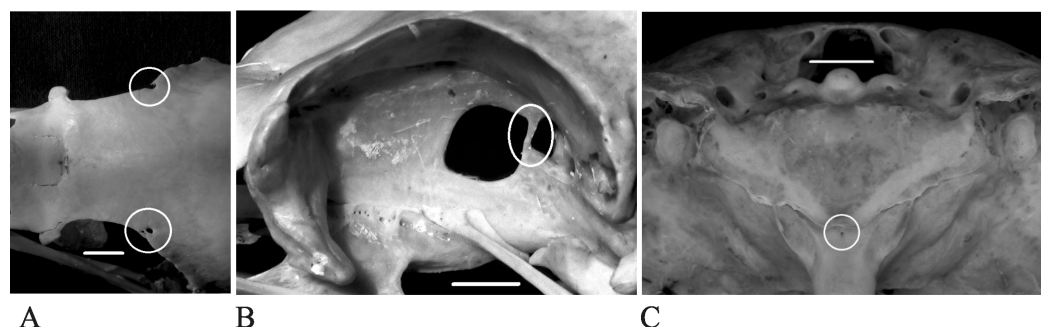


Fig. 2. A – Plan view, focusing on the frontal bone and its neighbours. SOF (Supraorbital foramen) were recognized on both sides of the supraorbital margin (circled). Scale bars (5 mm) are depicted in each figure. B – Left side view of the orbital cavity: Septum (in oval), osseous dissepiment separated the foramen opticum (left side hole) from the foramen neuro-ophthalmici (right side hole). C – Dorsal view. PPB (Pinhole in the parasphenoid bone) was observed (circled).

tions. The results generally coincided with those of previous phylogenetic studies based on mitochondrial DNA (STRINGER & MCKIE 1996; OPPENHEIMER 2004). Thus, the author applied the cranial phenetic approach in the current study. NAKAMURA and KRYUKOV (2015) were the first to apply this method to the field of ornithology; using three phenetic traits, the authors revealed a relationship among northern Jungle Crows populations. The current study focused on the same traits: supraorbital foramen (SOF), the septum in the inside orbital cavity (Septum) and the pinhole in the parasphenoid bone (PPB).

SOF was recorded as being present if any foramen on the supraorbital margin opened into the orbital cavity (Fig. 2A, in circles; present).

Septum was recorded as being present if an osseous dissepiment existed in the inside orbital cavity between the foramen opticum and the foramen neuro-ophthalmici (Fig. 2B, in oval; present).

PPB was recorded as being present if a pinhole existed in the parasphenoid bone at the bottom of the cranium near the front end of the lamina parasphenoidalis (Fig. 2C, in circle; present).

The incidence frequency of each trait was defined as $F = P/O$, where F = the frequency of occurrence for the trait (in percentage), P = the number of crania showing the trait (present) and O = the number of crania actually observed.

For the metric approach, the author selected the same characteristics as in his previously co-authored study (NAKAMURA & KRYUKOV 2016). Linear measurements were made with a digital caliper (error ± 0.1 mm). Landmarks for the measurements are shown in Fig. 3 A-B (MATSUOKA et al. 2009). The following measurements were taken from each skull, corresponding to the landmarks:

Cranium-L: cranium length [A-D]; A is the most posterior point of the prominentia cerebellaris, and D is the mid-point of the cranial-facial hinge.

Cranium-H: cranium height [B-C]. B is the bottom-side base on the lamina parasphenoidalis, while C is the highest counterpart of the cranial block.

Cranium-W: cranium width [K-K']. K is the most lateral right point of the processus postorbitalis; K' is its left-side counterpart.

Hinge-W: hinge width [J-J']. J is the most lateral right point of the cranio-facial hinge, while J' is its left-side counterpart.

Bill-L: bill length from the front end of the nostril [G-H]. G is the point on the right-side edge that corresponds to the front end of the nostril; H is the bill tip.

Bill-H: total maximum bill height [E-FF']. E is the point on the bill ridge that corresponds to the maximum bill height; F is its bottom-side counterpart on the right edge of the lower mandible, while F' is its counterpart on the left edge.

Bill-W: bill width at the front end of the nostril [G-G']. G is the point on the right-side edge that corresponds to the front end of the nostril; G' is its left-side counterpart.

Culmen-L: total culmen length [D-H]. D is the mid-point of the cranial-facial hinge; H is the bill tip.

Mandible-L: side length of the lower mandible [I-L]. I is the most anterior point of the rostrum mandibulae (the tip of the lower mandible); L is the most posterior point of the crista transversa fossae (the tail end of the lower mandible).

Bill aspect: Bill-H/Bill-L: this ratio represents the side view of the crow's facial profile. Larger values denote a more robust appearance, while smaller values indicate a more slender appearance.

Body mass: body mass was measured to the nearest 10 g with a spring scale.

Analysis of variance (ANOVA), logistic regression analysis, multivariate correlations analysis and a significant test of differences between means were all conducted using the programme JMP version 8.0.2.2 (SAS 2009).

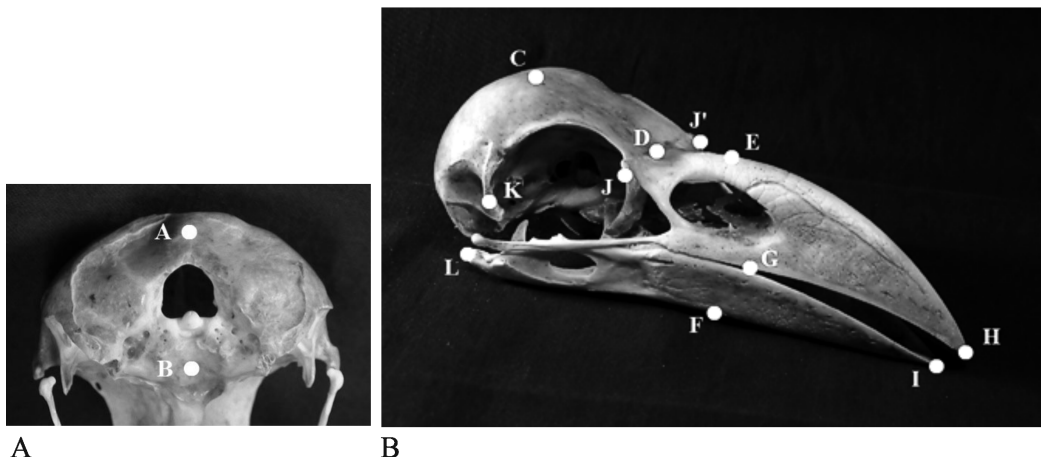


Fig. 3. A – Rear view, slanting to the bottom. B – Right side view, down and at a slant. Nine measurements for the landmarks were made as follows: Cranium-L (cranium length) [A-D], Cranium-H (cranium height) [B-C], Cranium-W (cranium width) [K-K'], Hinge-W (hinge width) [J-J'], Bill-L (bill length from the front end of the nostril) [G-H], Bill-H (total bill height) [E-FF'], Bill-W (bill width at the front end of the nostril) [G-G'], Culmen-L (total culmen length) [D-H] and Mandible-L (side length of the lower mandible) [I-L]. Landmarks for the left side are identified by letters with apostrophes (e.g. G').

These analyses were complemented with bioclimatic characteristics with the purpose of finding any climate-phenotype correlation (HIJMANS et al. 2005). Georeferenced presence points data (the identification and geographical location of each skull sample) were imported to DIVA-GIS; the presence points vector data were then combined with 19 forms of bioclimatic raster data based on common geographical locations. The combined data were extracted, and the extracted data were then analyzed by using JMP software. The spatial resolution of the bio-climatic data was 2.5 minutes, which corresponds to 4.65 km x 4.65 km = 21.62 km² at the equator (SCHELDEMAN & VAN ZONNEVELD 2010; HIJMANS et al. 2012). The bioclimatic analysis was adopted in the previous study dealing with a wide geographic range, from Upper Amur River basin to Hokkaido (NAKAMURA & KRRYUKOV 2016). In this study the range was restricted to Sakhalin Island and its surroundings.

III. RESULTS

The frequencies of the three nonmetric traits demonstrated nearly the same values between sexes (Table I). A simple logistic regression was conducted for both sexes to examine whether or not any tendencies existed related to the northern latitude. This nominal logistic regression estimates the probability of two response levels (present and non-present) as a continuous factor (latitudes). No significant fit was found by latitude for any trait (SOF: P = 0.899, 0.158; Septum: P = 0.087, 0.184; PPB: P = 0.620, 1.000, male and female respectively).

All of the comparisons of the ten morphometric characters and Body mass showed significant differences between males and females; the values of the males were larger than those of the females (Student’s t-test, *P*<0.05), except for bill aspect, where the males’ values were smaller than those of the females (NAKAMURA & KRYUKOV 2016). Scatterplot diagrams were drawn for both sexes in order to detect any signs of latitudinal cline; the northern latitude was plotted on the X-axis. Ten skull characteristics and Body mass were plotted on the Y-axis. The 10 skull characteristics were as follow: Cranium-L, Cranium-H, Cranium-W and Hinge-W from the cranial block; Bill-L, Bill-H, Bill-W, Culmen-L, Mandible-L and Bill aspect from the bill block (Fig. 4A. Cranium-L, B. Bill-L, C. Bill-H, D. Body

Table I

Frequencies of three nonmetric cranial traits of adult crows. P = number of crania showing trait (present); O = number of crania actually observed; some traits were not recorded in a few samples because of damage during cleaning. F = frequency of occurrence for the trait (%). Significance differences were calculated according to Fisher’s exact test (2-Tail)

Traits	Male		Female		Fisher’s exact test P
	P/O	F	P/O	F	
SOF (Supraorbital foramen)	24/33	73	23/30	77	0.778
Septum	7/34	21	6/29	21	1.000
PPB (Pinhole in the parasphenoid bone)	30/31	97	29/29	100	1.000

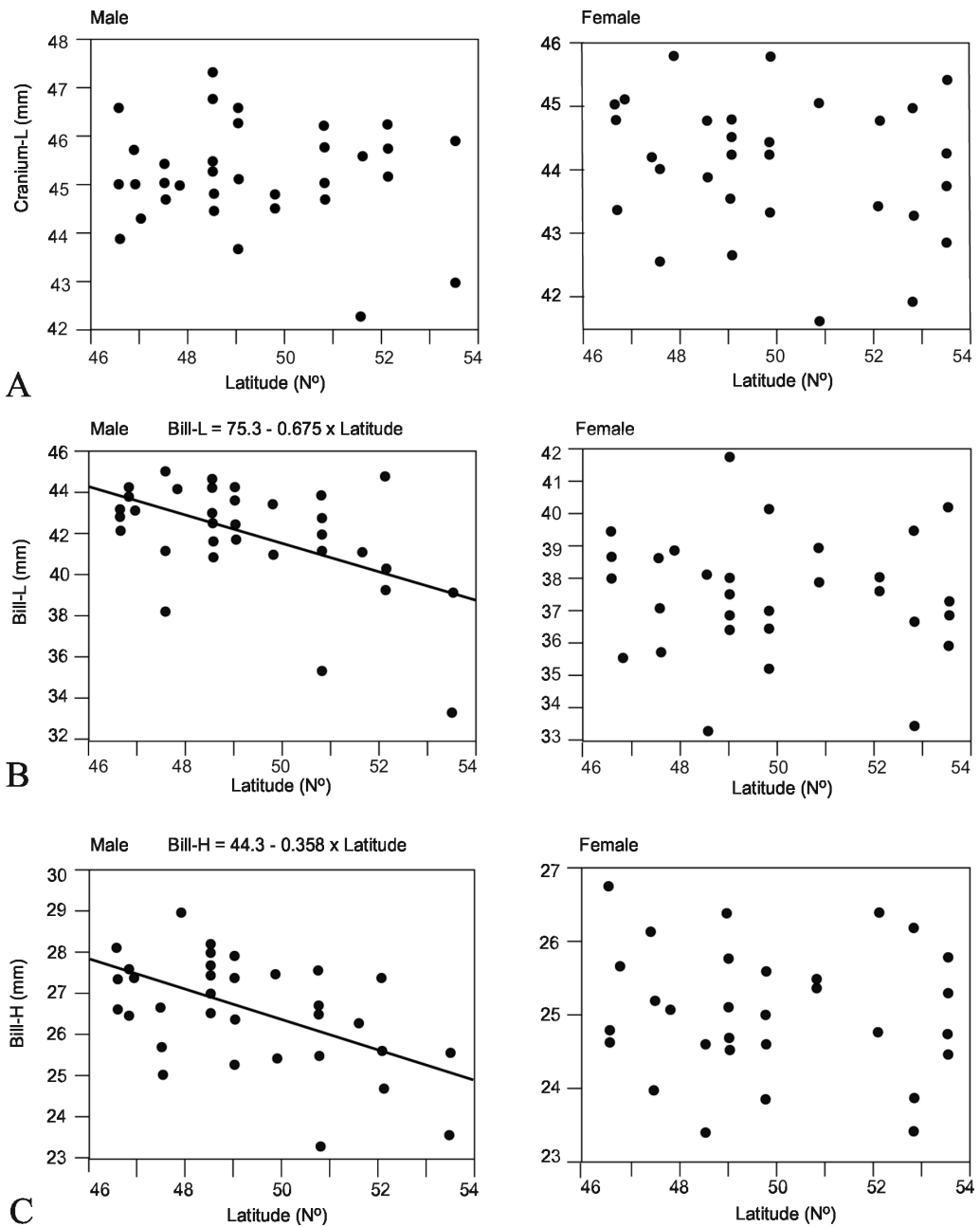


Fig. 4. Scatterplots of the northern latitudes (X axes) and three morphological measurements (Y axis). In the case of $P < 0.05$, an equation of linear fit is shown.

mass for both sexes are shown as examples). ANOVA was performed for both sample sets (Table II). In the male sample set, none of the cranium measurements (or the Bill aspect or Body mass) showed any clines, but all bill measurements showed a decreasing cline from south to north. In the female sample set, ten skull characters and Body mass showed no clines.

Table II

ANOVA of ten morphometric characteristics and Body mass by latitude. Significant P values are shown in bold. Sample sizes are in parentheses

Characteristics	Male		Female	
	(n = 33)		(n = 30)	
	R ²	P	R ²	P
Cranium block				
Cranium-L	0.0046	0.707	0.0160	0.522
Cranium-H	0.0809	0.109	0.0000	0.978
Cranium-W	0.1072	0.063	0.0002	0.940
Hinge-W	0.0116	0.551	0.0002	0.940
Bill block				
Bill-L	0.2800	0.002	0.0003	0.931
Bill-H	0.3084	0.001	0.0217	0.454
Bill-W	0.2565	0.003	0.0017	0.837
Culmen-L	0.2590	0.003	0.0106	0.602
Mandible-L	0.2409	0.004	0.0095	0.628
Bill-aspect	0.0363	0.288	0.0240	0.431
Body mass	0.0590	0.173	0.0169	0.509

The next question to be addressed was to determine which climatic factors were associated with this latitudinal cline. The author tried a bioclimatic analysis focusing on Sakhalin Island. A multivariate correlations table of 19 bioclimatic characters and latitude was examined to determine these factors. BIO4 (temperature seasonality with a standard deviation of monthly temperature (°C)²) scored the highest correlations (Table III). The spatial configuration of the climatic seasonality of temperature (BIO4) was then drawn (Fig. 5). A clearly increasing gradation from south to north was found: the farther north the latitude, the larger the temperature instability.

Table III

Multivariate correlations between the 19 bioclimatic Variables and the latitude

The 19 Bioclimatic Variables and their definitions		Latitude
BIO1	Mean annual temperature	-0.796
BIO2	Mean diurnal range (mean of max. temp – min. temp)	0.311
BIO3	Isothermality (BIO2/BIO7)(*100)	-0.537
BIO4	Temperature seasonality (coefficient of variation)	0.974
BIO5	Max. temperature of warmest month	-0.124
BIO6	Min. temperature of coldest month	-0.770
BIO7	Temperature annual range (BIO5 – BIO6)	0.834
BIO8	Mean temperature of the wettest quarter	-0.683
BIO9	Mean temperature of the driest quarter	-0.824
BIO10	Mean temperature of the warmest quarter	-0.321
BIO11	Mean temperature of the coldest quarter	-0.869
BIO12	Total (annual) precipitation	-0.867
BIO13	Precipitation of wettest month	-0.755
BIO14	Precipitation of driest month	-0.260
BIO15	Precipitation seasonality (coefficient of variation)	0.099
BIO16	Precipitation of wettest quarter	-0.802
BIO17	Precipitation of driest quarter	-0.531
BIO18	Precipitation of warmest quarter	-0.875
BIO19	Precipitation of coldest quarter	-0.555

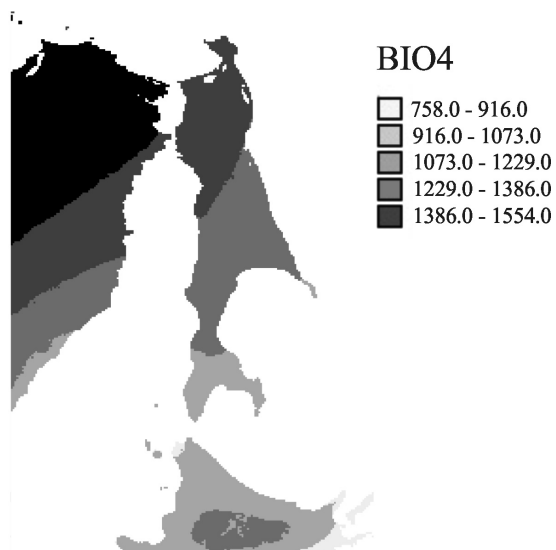


Fig. 5. Spatial configuration of the climatic seasonality of temperature (standard deviation of monthly temperature, (°C)²). Darker colours indicate regions with higher seasonal deviation. Seasonality increases from south to north.

IV. DISCUSSION

In physical anthropology, SOF is considered to be closely related to genetic background; its incidence frequency is relatively independent of environmental conditions such as diet (DODO & ISHIDA 1990; OSSENBERG et al. 2006). SOF, Septum and PPB have not been studied before in ornithology, and their functions are thus not yet known. The three phenetic traits did not show a latitudinal variation in the logistic analysis of the current study, which suggests that Jungle Crows exchange genes freely on Sakhalin Island.

All five bill parameters demonstrated a decreasing cline from south to north only in the males (Table II, Fig. 4). One might wonder why male's bills become smaller along with higher latitude. The conventional view is that the clines have evolved in relation to dietary type (LACK 1947). The Jungle Crow is a generalist feeder, and no reports to date have confirmed a sexual difference in feeding behaviour. Instead of feeding, the role of heat regulation must be important, because *mandshuricus* crows inhabit the northernmost area of the Jungle Crows' distribution range (Fig. 1). The bill protrudes from the trunk; in cold conditions, the heat loss from this organ is considerable (HAGAN & HEATH 1980; SYMONDS & TATTERSALL 2010; MCCAFFERTY et al. 2013). The smaller bill of northern crows would thus be advantageous under such conditions. In contrast, none of the four cranial parameters showed any latitudinal clines for either sex. The cranium occurs between the trunk and the bill, and it is feathered completely except for the eyes. As such, adaptation to cold ambient temperature is not as urgent as it is for the bill.

Two plausible reasons could help to explain the male-biased latitudinal cline in bill characteristics, as follows: (1) if young male crows tend to settle in their natal region, and young female crows disperse widely. Environmental temperature plays a key role in shaping bill size among birds: those raised in cold temperature would develop smaller bills than those reared in warm climates (BUMESS et al. 2013). And (2) if male crows are inclined to stay longer in their territory during the migration season and female crows tend to leave for longer periods of time. In Norway, SLAGSVOLD (1982) studied the migration behavior of Hooded Crows *C. corone cornix*. The author found that juveniles and adult females migrated south for longer distances and stayed away longer than adult males in the winter. As a result, more adult males were exposed to the cold climate than adult females. In Sakhalin Island, however, the juvenile's settlement process and the migration behaviour of Jungle Crows are not well-known; the cause of the male biased latitudinal cline should be left in open question.

In the current study's supplemental analysis via bioclimatic characteristics, BIO4 (temperature seasonality) scored the highest correlation with a northern latitude (Table III). Though many bioclimatic characteristics showed high correlation with latitude, the author considers that BIO4 is the most important variable for generating the latitudinal cline, because the definition of BIO4 implies its comprehensiveness (i.e. it contains other variable characteristics implicitly). The male-biased cline, decreasing from south to north, coincided in a reverse relationship with the temperature seasonality (Fig. 5); the darker colours indicate regions with higher seasonal deviations. Seasonality increases were from south to north. Allen's rule may give an explanation for the significant relationships between male bill and both latitude and BIO4.

Although previous studies have supposed a trend to a reversed Bergmann's rule on Sakhalin Island (KURODA 1970; IWASA et al. 2002), neither of the cranial block characteristics nor Body mass showed this trend in the current study (Fig. 4d). In general, in concordance with Bergmann's rule or the reversed Bergmann's rule, populations must be isolated for long periods of time for morphological differences to become fixed; Sakhalin Island, however, lacks the geographic barriers to sustain such isolated populations.

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APPENDIX

Summary of sampling. Localities with latitude (°N), longitude (°E), sample sizes with male and female respectively. The collection work began on June 27 of 2007 and was finished on July 10. This period corresponds to late breeding season (NECHAEV 1991)

Location	Latitude	Longitude	Sample size	
			male	female
Kholmsk	46.8	142	1	1
Aniva	46.8	142	4	3
Yuzhno-Sakhalinsk	46.9	142.3	1	—
Dolinsk	47.4	142.5	—	1
Starodubskoye	47.5	142.6	2	1
Tomari	47.8	142.2	1	1
Voctochnyy	48.5	142.7	6	2
Poronaysk	49	142.8	5	5
Smirnykh	49.8	142.9	2	4
Timovskoye	50.8	142.5	5	2
Argi-Pagi	51.6	142.5	1	—
Nogliki	52.1	143	*5	2
Val	52.8	142.8	—	3
Tungor	53.5	142.8	1	2
Okha	53.5	142.8	—	3

* One heavily damaged male skull from Nogliki was not used in the cranio-metric analysis.